The Ciliated Protozoa

CHARACTERIZATION, CLASSIFICATION, AND GUIDE TO THE LITERATURE

John O. Corliss

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PREFACE

THE ciliated protozoa have not been treated monographically, within the confines of a single study, since the encyclopedic works of Bütschli (1887–1889) and Kahl (1930–1935). Even the more recent of these, the invaluable keys and diagnoses by Kahl, omitted consideration of certain parasitic groups and the marine tintinnids. Also, since 1935, the number of taxa of ciliates has nearly doubled at every level below the ordinal group: in families, genera, and species. In the meantime, furthermore, important revisions in the scheme of classification of these protozoa, essentially the first major changes since the time of Stein (1867), have been proposed. But these suggested revisions, and the hypotheses upon which they are based, have never been presented and discussed extensively in any single paper.

It is time to at least stop and take stock. New genera and families need to be fitted into the framework of the proposed classificational scheme endorsed in the present study. It is becoming increasingly difficult to undertake comparative taxonomic studies today until we have gained a broader background knowledge of the current over-all problems facing the ciliate systematist.

The present work represents an attempt to carry out three main objectives: to offer concise characterizations of the major taxa comprising the new scheme of classification; to present an up-to-date list of all the described genera of ciliates considered acceptable; and to include annotated reference to all significant, sizeable works, including the most recent, in the principal areas of research in ciliate protozoology. Major concepts are illustrated and "typical" or representative genera are figured. Particular attention is given to nomenclatural problems, since a number of these have gone unattended for many years.

It is earnestly hoped that specialists in all areas, perhaps in systematics above all, will attack with renewed vigor the many important problems remaining to be done. Certainly the present work has revealed more problems than it has solved.

I am indebted to many persons for concrete assistance during the preparation of this work. Specifically I must at least mention my deep gratitude to Professor E. Fauré-Fremiet, Paris, for his constantly stimulating help, advice, and encouragement first given me during my stay in his laboratories at the Collège de France and at Concarneau, 1951–1952, and continued ever since that most profitable year; to my research assistants and graduate students at the University of Illinois, in particular Miss Margaret Dysart, Miss Louise Weisberg, and Mr. Jacques Berger, for their unstinting aid, especially in checking the bibliographical material involved; to Mr. Lyle Bamber and the library staffs at the University of Illinois for their well-stocked stacks and their patient assistance in locating rare or obscure publications; to Miss Alice Boatright, for her painstaking and most sympathetic execution of all the drawings used here; to Mrs. Ruth Bruckner and Mrs. Suzanne Ford for such cheerful diligence in typing the manuscript; to my understanding wife, Dorothy, for her unselfish moral support in particular; and to Professor P. B. Medawar, University College London, for graciously providing accommodation in his Department of Zoology during completion of the book while I was on sabbatical leave from the University of Illinois, 1960–1961. Finally, I wish to acknowledge the indispensable aid of grants from the National Science Foundation, Washington, D.C.

JOHN O. CORLISS

CONTENTS

CHAPTER 1

INTRODUCTORY CONSIDERATIONS

THERE is a definite need for revision of the systematics of the ciliates. Extant schemes of classification of this circumscribed assemblage of protozoa stem principally from the authoritative 19th century treatises of Stein, Bütschli, and Schewiakoff. Even the most modern comprehensive taxonomic monographs available, the prodigious works of Kahl, appeared over a quarter of a century ago. In the meantime innumerable descriptions of new ciliates have been published, improved techniques of study have been devised, new ideas of importance concerning phylogenetic interrelationships have been promulgated. This great accumulation of pertinent data has yet to be digested and carefully incorporated into a revised classificational system of the entire subphylum Ciliophora.

In the present section of this book concise, up-to-date characterizations of the major ciliate groups, accompanied by illustrations of representative genera, are presented in the framework of such a new scheme of classification. Key references to the literature concerned with the biology and systematics of these groups are included, but generally limited to works published within the past twenty-five or thirty years; in fact, the emphasis is on the results of researches completed within the past decade. The invaluable older literature is not neglected in this book, but citation of such papers is reserved primarily for Part III.

The general classificational system followed in Chapters 1–9 is extended and applied to the lower taxonomic levels in Part II, where families and their included genera are considered and where pertinent nomenclatural details are supplied for all taxa.

The final chapter of the present section is devoted to brief treatment of the evolutionary and phylogenetic problems which have influenced the structure of the new classification.

What are the bases for suggesting *any* major changes over conventional classificational schemes? And what is the nature of the specific revision endorsed in this book? These questions recently have been discussed elsewhere (Corliss, 1956a, 1959b, 1960c) and therefore need to be considered only briefly here. Appropriate examples illustrating the several main points made below are provided in the figures of Plates I–VIII.

Bases for Revisions

1. Emphasis on the infraciliature, as opposed to the externally visible ciliature, in comparative morphological and morphogenetic studies. The infraciliature, consisting essentially of the subpellicularly located basal granules or kinetosomes and associated fibrils of both the somatic and buccal ciliature, has been found to be a more conservative, universal property of ciliates. Thus it is considered a fundamental characteristic of greater reliability in

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Explanation of Plate I opposite

Photomicrographs, entirely unretouched, of various ciliates impregnated with silver according to the Chatton–Lwoff technique [from Corliss (1959b)].

Fig. 1. A group of *Tetrahymena pyriformis*, showing a number of features of their silverline system: ciliary meridians (longitudinal rows of the argentophilic basal granules or kinetosomes), buccal infraciliature in the oral area of the body, pair of contractile vacuole pores, cytoproct, etc. Fig. 2. Ventral view of *T. setifera*, showing silverline structures at a higher magnification.

Fig. 3. Apico-ventral view of *T.* sp., revealing particularly the infraciliary bases of the AZM (adoral zone of membranelles) in the buccal cavity. Fig. 4. Subequatorial view of the ventral surface of *T. pyriformis* in an early stage of binary fission; note that stomatogenesis has nearly been completed in the posterior filial product, the opisthe. Fig. 5. Apical view of one of the products of division of *T. patula*, depicting clearly the tetrahymenal organization of the buccal apparatus.

Fig. 6. Ventral view of *Glaucoma scintillans*, at a deep focal level which shows the bases of the tripartite AZM with diagrammatic clarity. Figs. 7 and 8. Ventral views of *Euplotes* spp., revealing the infraciliary bases of the somatic cirri and the buccal membranelles; the longitudinal rows of argentophilic granules seen here, bases of the so-called sensory bristles, are showing through from the dorsal surface of these dorso-ventrally flattened ciliates.

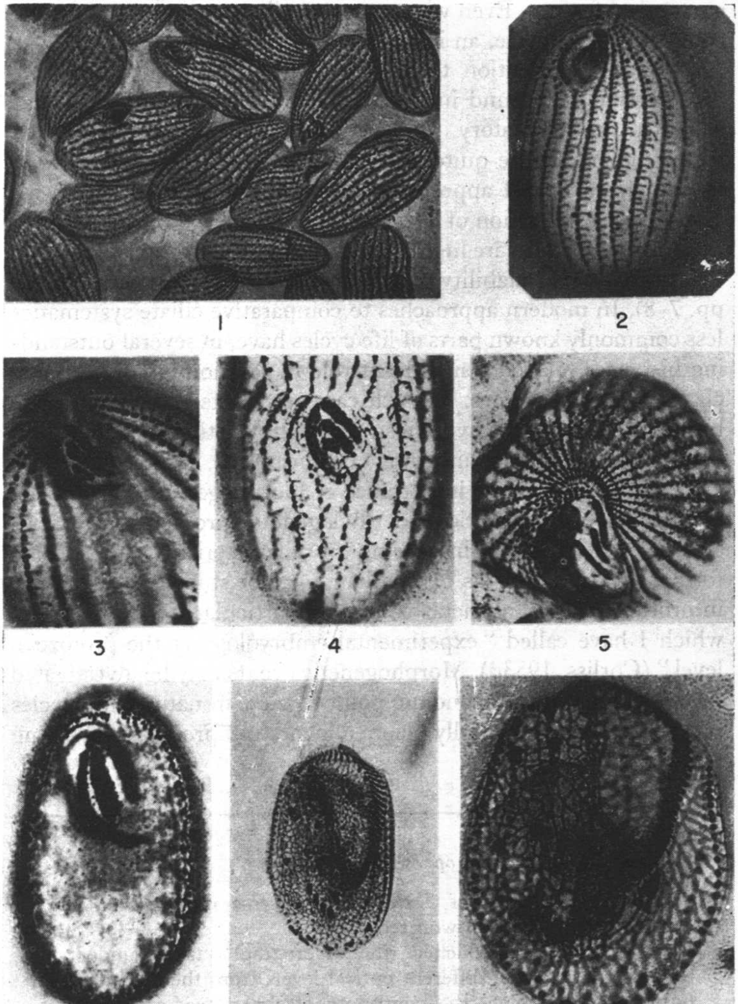

PLATE I

comparative taxonomic investigations than any other single anatomical feature. Even when external ciliature is absent in some stage of the life cycle, an infraciliature persists.

2. Renewed attention to full life cycles. The forms of ciliates most commonly found in nature generally represent "mature" stages in the life history. As has long been known, study of such forms alone may be quite misleading from the point of view of the organism's most appropriate taxonomic position. Discovery and proper recognition of "larval" or other developmental stages in ciliate ontogenies are highly desirable and are of particular value today with the availability of new techniques and hypotheses (see pp. 7–8). In modern approaches to comparative ciliate systematics less commonly known parts of life cycles have, in several outstanding instances, played a significant role in revision of conventional classificational schemes. In such cases the facts discovered have been coupled with the hypothesis that ontogenetic stages may hold clues of phylogenetic, and thus classificational, value.

3. Realization of the importance of morphogenetic phenomena in solution of systematic and phylogenetic problems. Morphogenesis, "the coming-into-being of characteristic and specific form in living organisms" (Needham), can be studied to advantage in protozoa as well as metazoa. This is particularly true in studies which I have called "experimental embryology at the protozoan level" (Corliss, 1953d). Morphogenetic events may be investigated from a comparative taxonomic point of view in natural life cycles as well as in experimentally planned laboratory problems involving regeneration, etc.

Explanation of Plate II opposite

A single specimen of *Tetrahymena setifera* impregnated with silver by the Chatton–Lwoff technique.

FIGS. 1–12. Unretouched photomicrographs taken under oil immersion at twelve different optical levels from the apical to the posterior pole. Note the continuity of the ciliary meridians or kineties down the entire length of the organism's body. The prominent dark spot marks the location of the oral apparatus; the centrally located dark area in FIGS. 9–11 represents the macronucleus.

[I am indebted to Mr. Luis de la Torre for preparation of this unusual set of photomicrographs.]

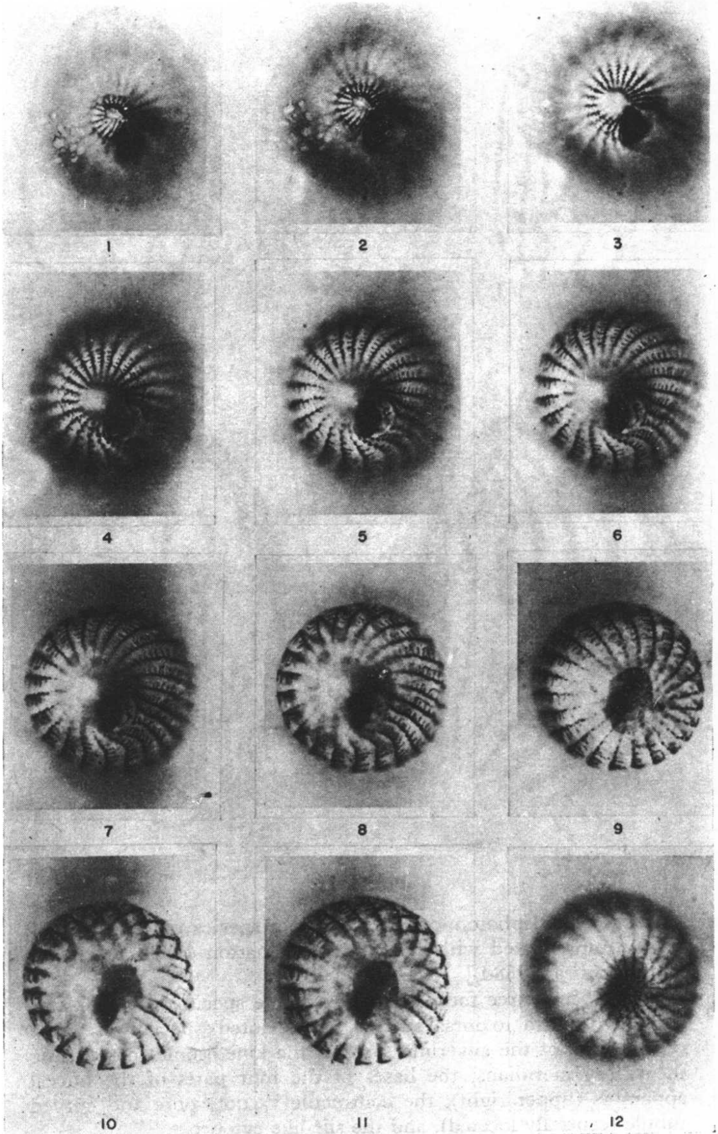

PLATE II

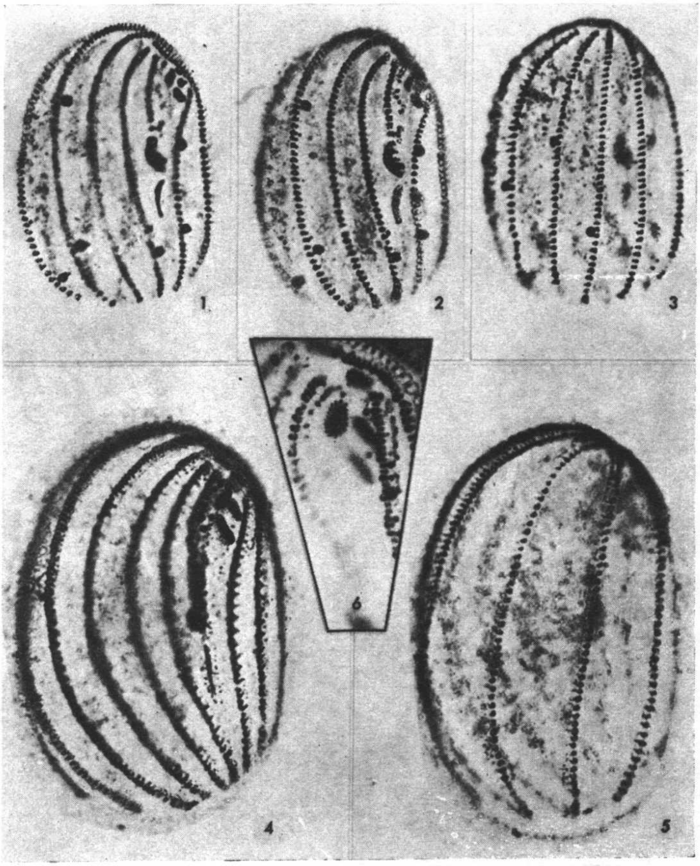

PLATE III

Unretouched photomicrographs of two species of *Pseudomicrothorax* impregnated with silver by the Chatton–Lwoff technique [from Corliss (1958d)].

FIGS. 1–3. Three focal levels of a single specimen of *P. agilis*, from high ventral to dorsal surface. To be noted especially are these components of the silverline system: the kinetosomes comprising the ciliary meridians, the bases of the four parts of the buccal apparatus (upper right), the contractile vacuole pore and curved tubule (centrally located), and the slit-like cytoproct.

FIGS. 4–6. Ventral and dorsal surfaces of *P. dubius*, showing the

4. Recognition of homologous structures in ciliates assigned to different taxonomic groups. There has long been a natural tendency among specialists to develop a particular terminology for characteristics revealed in studies of a circumscribed group without an attempt to consider the possible homologies with features exhibited by organisms belonging to the other major taxa within the same subphylum. This has especially been true with regard to structures in the oral region, and an extensive " mouth-part terminology " has impeded our taxonomic progress because it has not allowed ready recognition of identical or homologous features possessed in common by diverse ciliates (Corliss, 1955b, 1959b; Fauré-Fremiet, 1961).

5. Application of new techniques of study. Foremost among these must be mentioned the discovery of methods of silver impregnation, since the ciliary basal granules were found to be argentophilic. Thus the infraciliature could be studied intensively during all stages in the life cycle, morphogenetic events could be examined in detail, mouth-part structures could be elucidated with precision. Leaders in development of these all-important silver techniques include Klein, who discovered the dry method in 1926 in Vienna; von Gelei, who used modifications of the technique in an impressive series of investigations carried out in Hungary; and Chatton and Lwoff, who produced the French refinement which has played the most significant part of all in comparative studies of ciliates since 1930. (See Part III for further discussion of specific contributions of these protozoologists.) Within the past decade electron microscopical investigations, now steadily on the increase, have begun to serve as an indication that ultrastructural studies will be of considerable value in systematic work of the future.

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same anatomical features just noted. In the enlarged picture of the buccal area (FIG. 6) may be detected the proximal ends of the so-called trichites comprising the armature of the organism's cytostome-cytopharyngeal complex. It is the simultaneous possession of a hymenostome-like AZM and UM (adoral zone of membranelles and undulating membrane) plus the gymnostome-like cytopharyngeal trichites that places *Pseudomicrothorax* in the possible role of a taxonomic " missing link " (see text).

6. Promulgation of new hypotheses plus reinterpretation of older ones. Most important in this connection have been the heuristic ideas of Chatton and Fauré-Fremiet (see Corliss, 1956a, for specific consideration of these proposals; and see citations in Part III). Hypotheses of greatest significance in revision of conventional ciliate schemes of classification include: the autonomy and genetic continuity of the kinety (the infraciliary basal granules or kinetosomes plus associated fibrils or kinetodesmata); the rule of desmodexy (the kinetodesma lies to the right of its row of kinetosomes); the pluripotency of the kinetosome in morphogenetic phenomena (such as new mouth formation or stomatogenesis); the

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Explanation of Plate IV opposite

Drawings of various features of taxonomic importance which comprise the silverline system of ciliates.

FIG. 1. Ventral view of a dividing *Tetrahymena pyriformis*, showing diagrammatically the primary meridians formed by the rows of argentophilic basal granules or kinetosomes and the essential infraciliary structures of the tetrahymenal buccal apparatus in both the proter and the opisthe [redrawn from Corliss (1952a)]. FIG. 2. Enlargement of the anterior end of the ventral surface of the same species; the lines coursing between the primary meridians represent the argentophilic but generally non-granular secondary meridians [redrawn from Corliss (1953a)].

FIG. 3. Posterior polar view of *T. pyriformis*, showing details of structures revealed by silver impregnation: note particularly the primary and secondary meridians, the two contractile vacuole pores, and the single cytoproct [from Holz and Corliss (1956), originally redrawn from Corliss (1952a)]. FIG. 4. Posterior polar view of *T. setifera*, showing the same details as mentioned for Fig. 3 plus the prominent polar basal granule-complex which represents the infraciliature of the long caudal cilium possessed by this species [redrawn from Holz and Corliss (1956)].

FIG. 5. Ventral view of *Euplotes eurystomus*, showing particularly the prominent infraciliary bases of the cirri, the bases of the individual parts of the AZM (adoral zone of membranelles), and the " chicken-wire " mesh-work of argentophilic fibres(?) all over the surface [redrawn from Chatton and Séguéla (1940)]. FIG. 6. Dorsal view of the same silver-impregnated specimen of *E. eurystomus:* note especially the rows of the bases of the so-called sensory bristles; the short black lines at the anterior end represent an extension of the AZM from the ventral surface [redrawn from Chatton and Séguéla (1940)].

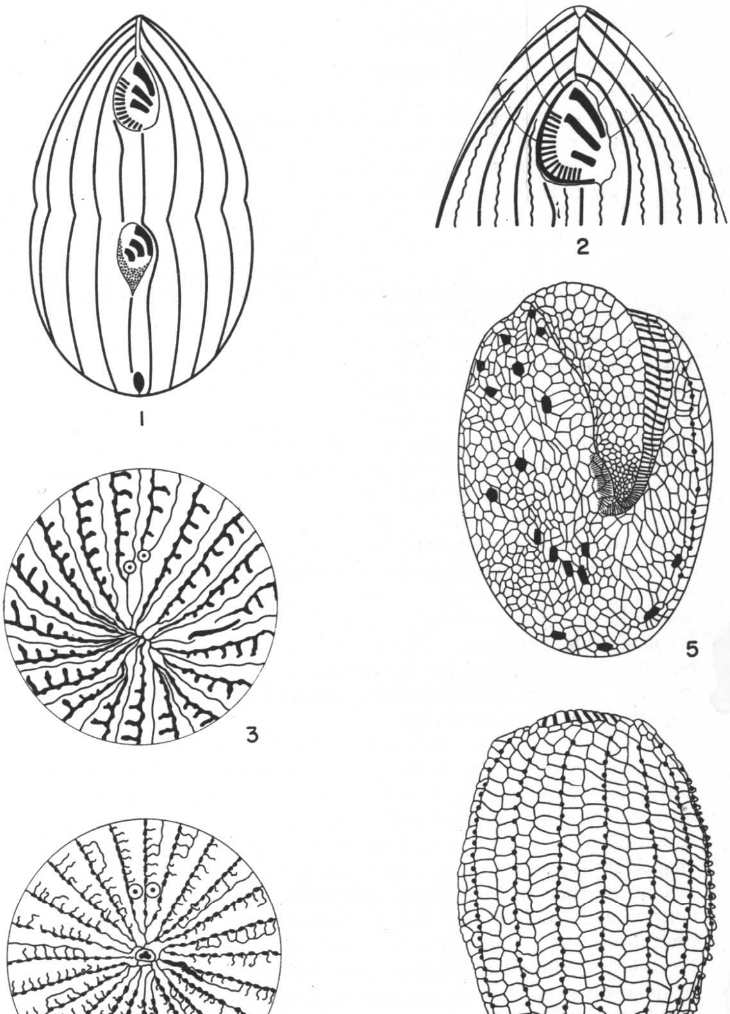

PLATE IV

Explanation of Plate V opposite

Illustration of certain concepts of value in ciliate systematics (see also Pls. VI–IX).

FIGS. 1–3. The " Rule of Desmodexy," illustrating the independence and polarity of the kinety — the all-important infraciliary structure comprised of the allegedly autonomous, self-duplicating argentophilic basal granules or kinetosomes plus the argentophobic kinetodesma which always lies to the (organism's) right of the associated kinetosomes [modified from figures in Chatton and Lwoff (1935b)]. FIG. 1. View of the left side of a ciliate such as *Tetrahymena*, showing diagrammatically the path of a kinety on this side and also, depicted with a lighter line and circles instead of dots, the path of a kinety on the opposite (right) side of the organism, as it would be seen *through* the body. Two points, especially, should be noted: the position of the kinetodesma to the right of the line of kinetosomes, endowing the organism with polarity; the independence, at both poles of the body, of the two kineties shown. In reproduction of the ciliate the kineties are transected (" perkinetal fission "), replacing their missing halves with subsequent growth. FIG. 2. Apical polar view, illustrating how the rule of desmodexy shows the absolute impossibility of continuity " over the top " of the two kineties coursing poleward from left and right sides of the body: if the kinetodesmata were one (i.e., united), the kinetosomes would have to jump across the single kinetodesma at the pole, an inconceivable situation. FIG. 3. Posterior polar view, offering equally strong support for the independence of the longitudinal kineties. Modern electron microscopical studies have verified this important Chattonian concept.

FIGS. 4 and 5. The contrast between homothetogenic and symmetrogenic types of fission [figures original but based on text and diagrams offered by Chatton and Villeneuve (1937)]. FIG. 4. View of the right side of a ciliate such as *Tetrahymena*, a stage late in fission. The condition of homothety is ideally illustrated in the shapes and locations of the two oral areas and of various silverline structures such as the ciliary meridians, the cytoproct, and the contractile vacuole pores. FIG. 5. View of fission in a generalized phytoflagellate. The symmetrogenic or mirror-image type of division is deliberately idealized here for sake of contrast. Even as many ciliates fail to demonstrate perfect homothetogenic fission, flagellates may not show completely mirror-image duplication of cytoplasmic organelles. Such modifications or exceptions, however, probably should not be considered to invalidate the basic Chattonian hypotheses involved.

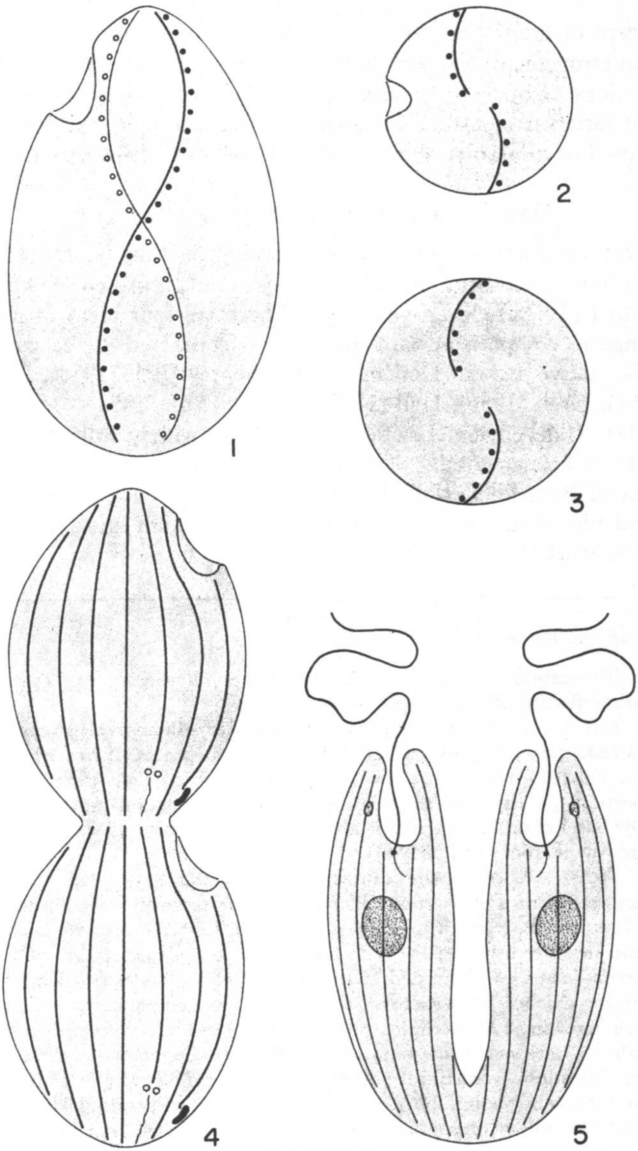

PLATE V